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Capreolus pygargus.

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Capreolus Gray, 1821

Capreolus Frisch, 1775:2.
Capreolus Gray, 1821:307. Type species *Cervus capreolus* Linnaeus, 1758:68.
Caprea Ogilby, 1836:135.

CONTEXT AND CONTENT. Order Artiodactyla, Suborder Ruminantia, Family Cervidae, Subfamily Odocoileinae, Tribe Capreolini (Simpson, 1945). The genus *Capreolus* presently includes two extant species: *Capreolus pygargus* and *Capreolus capreolus* (Sokolov et al., 1992). A key to species follows:

Size moderate to large, coloration of head and metatarsal glands generally not different from trunk, beams of antlers set far apart, chromosome set exhibits B-chromosomes ..... *Capreolus pygargus*

Size small, head and metatarsal glands darker than trunk, beams of antlers not far apart, chromosome set has no additional B-chromosomes ..... *Capreolus capreolus*

Capreolus pygargus Pallas, 1771

Siberian Roe Deer

Cervus pygargus Pallas, 1771:453. Type locality "Right bank of river Sok, Trans-Volga area, Russia."
Capreolus tianschanicus Satunin, 1906:527. Type locality "Kuldja, Tien-Shan."
Capreolus bedfordi Thomas, 1908:645. Type locality "Mt. Chao-Cheng-Shan, 100 miles west-north-west of Taiyuenfu, Shansi, China."
Capreolus pygargus var. *ferganicus* Rasewig, 1909:16. Type locality "Fergana," Turkestan.
Capreolus pygargus Pall. var. *caucasica* Dinnik, 1910:66. Type locality "Northern Caucasus."
Capreolus melanotis Miller, 1911:231. Type locality "Thirty miles east of Ching-yang-fu, Kansu, China."
Capreolus capreolus ochracea Barclay, 1935:627. Type locality "Korea."

CONTEXT AND CONTENT. Context as in generic summary of the genus *Capreolus*. Two well-defined subspecies of *C. pygargus* are recognized (Danilkin, 1989a; Sokolov et al., 1992):

C. p. pygargus Pallas, 1771:453. See above. Includes *caucasica*.
C. p. tianschanicus Satunin, 1906:527. See above. Includes *bedfordi*, *ferganicus*, *melanotis*, and *ochracea*.

DIAGNOSIS. *Capreolus pygargus* is distinguished from *C. capreolus* by larger size of body, cranium, and antlers. Here measurements for nine *C. pygargus* populations (body measurements, and body mass from 262–299 individuals per population, $n = 521$ for skull measurements), with comparable values for eleven *C. capreolus* populations (body measurements and body mass for 948–2,801 individuals per population, $n = 598$ for skull measurements) in parentheses, are as follows: total length, 126–144 cm (107–126 cm); shoulder height, 82–94 cm (66–83 cm); body mass, 32–48 kg (22–32 kg); condylobasal length of skull, 201–231 mm (179–200 mm); maximum length of nasal bones, 69–80 mm (51–66 mm); length of lower tooth row, 71–76 mm (61–67 mm); maximum length of antlers, 276–333 mm (184–258 mm); maximum antler-to-antler distance, 168–257 mm (76–139 mm; Danilkin et al., 1992b). Auditory bullae of deer are larger and noticeably protrude from the bullar fossa.

Capreolus pygargus also differs from *C. capreolus* in coloration of the head and metatarsal glands. In *C. pygargus*, the summer coat of the head is uniformly reddish or grey-reddish, but in *C. capreolus*, it is gray or gray-brown (Flerov, 1952; Heptner et al., 1961). *C. capreolus* has a light nose patch (lacking in *C. pygargus*) and brown or dark-brown metatarsal gland hair (Stubbe, 1990). Metatarsal gland hair of *C. pygargus* is reddish (Gromov, 1986). The karyotype of *C. pygargus* exhibits an extra B-chromosome (Danilkin, 1985*b*; Sokolov et al., 1978) that is lacking in *C. capreolus* (Gustavsson, 1965).

GENERAL CHARACTERS. Siberian roe deer are telemetacarpalian deer of moderate size (Fig. 1). Their front legs are shorter than the hind ones, the neck is long, there is no mane, the ears are fairly large (13–15 cm), and the tail is rudimentary (2–4 cm), as are the preorbital glands. The winter pelage in northern populations is light gray, but grayish-brown and ochraceous in southern populations. The belly is creamy. The caudal patch is white. In summer, the coat is reddish and the white caudal patch is less pronounced or absent. Young are spotted.

Males are slightly larger than females and have three-tined antlers (Fig. 2), which are widely spaced at the base, slant upward, and are strongly tuberculated. Antlers are shed in autumn or early winter and begin to regrow immediately after shedding (Flerov, 1952; Heptner et al., 1961; Smirnov, 1978). Mean measurements from nine different populations for females (body measurements and body mass from 124–137 individuals per population, $n = 220$ for skull measurements), with comparable values for males (body measurements and body mass for 138–162 individuals per population, $n = 301$ for skull measurements) in parentheses are as follows: total length, 126.7–144.4 cm (128.1–143.8 cm); shoulder height, 81.7–91 cm (83.1–94.1 cm); body mass, 32–46.9 kg (34.9–48.6 kg); maximum skull length, 219.3–238.8 mm (213.8–244.1 mm); maximum skull width, 92.2–99.5 mm (94.8–106.1 mm; Danilkin at al., 1992*b*).

The two subspecies of Siberian roe deer are morphologically and genetically distinct. Mean measurements from three different populations of *C. p. pygargus* ($n = 102$ for body measurements and body mass $n = 182$ for skull measurements) with comparable values for five populations of *C. p. tianschanicus* (body measurements and body mass for 141–173 individuals per population, $n = 259$ for skull measurements) in parentheses are as follows: mean total length, 140–144 cm (126–137 cm); body mass, 41–48 kg (32–40 kg); condylobasal length of skull, 223–231 mm (201–218

FIG. 1. Male *Capreolus pygargus* from Tien-Schan area. Photograph by A. Danilkin.

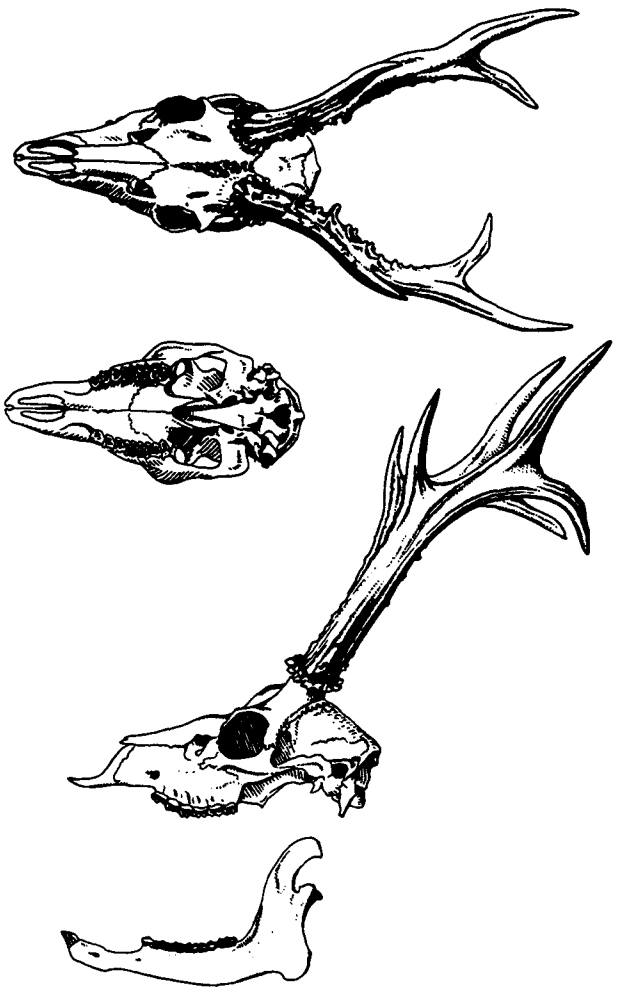

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Capreolus pygargus* (male from the Samara district, Trans-Volga area, Russia). Personal collection by A. Danilkin. Greatest length of cranium is 247.5 mm. Drawing by V. M. Gudkov.

mm); facial length, 125–127 mm (110–120 mm); length of nasal bones, 78–80 mm (68–76 mm); length of mandible, 189–194 mm (168–183 mm); distance between external sides of the axial shafts of antlers, usually >74 mm (usually <74 mm). The karyotype of *C. p. pygargus* normally exhibits 1–4 B-chromosomes, while that of *C. p. tianschanicus* usually exhibits 5–14 B-chromosomes. Siberian roe deer from the Altai are intermediate in size and exhibit variable numbers of B-chromosomes (Danilkin et al., 1992*b*; Markov, 1985).

DISTRIBUTION. Siberian roe deer range throughout the temperate zone of eastern Europe and Asia (Fig. 3). Fossil records and reports of naturalists indicate that a century ago the Don River was the western boundary of the distribution and that these ungulates reached the northern Caucasus (Korotkevich and Danilkin, 1992). The greatest change in range occurred during the late 19th and early 20th century when the species was eradicated by overhunting in eastern Europe, northern Kazakhstan, western Siberia, and in northern regions of eastern Siberia. As a result, the range was divided into two parts (Ural and Siberia; Heptner et al., 1961). Protective measures have resulted in almost complete recovery of the historic distribution. The western edge is defined by the Khoper River and Don River bend, where there is a zone of contact with *C. capreolus*. A large portion of the restored range of Siberian roe deer resulted from introductions on the Stavropol Upland (north of Caucasus Range; Danilkin, 1985a).

Distributional boundaries fluctuate with seasonal migrations, particularly in Asia. Main factors that limit movement are snow depth and duration of snow cover; e.g., snow-covered mountain massifs are a considerable barrier. There is a discontinuity in the range caused by the Altai, western and eastern Sayan Ranges, Lake Baikal, Stanovoi Plateau and Stanovoi Range (Fig. 3). Ecogeographical isolation has promoted morphophysiological differentiation of northern and southern populations of deer, which are recognized as being subspecifically distinct (Danilkin, 1989b, 1992d).

FOSSIL RECORD. Similarities in skull, tooth, and antler morphology suggest that Pliocene species of genus *Procapreolus* were immediate predecessors of *Capreolus* (Korotkevich, 1970; Korotkevich and Danilkin, 1992). The evolutionary transformation of *Procapreolus* was likely promoted by gradual changes in climate from subtropical to temperate, accompanied by steppe formation (Korotkevich, 1970).

Early Pleistocene remains of *Capreolus*, the most ancient in Asia, have been found in Eastern Kazakhstan (Vislobokova, 1973). However, because fossils are sparse and only tentatively aged, it is hard to determine time of appearance of roe deer in any given region of Eurasia. Since natural (glacial and aquatic) barriers existed on the boundary between Europe and Asia in Pleistocene, there are grounds for believing that European roe deer were isolated from Siberian roe deer for a long period, resulting in substantial genetic differences and partial reproductive isolation (Korotkevich and Danilkin, 1992).

FORM AND FUNCTION. *Capreolus pygargus* has a light slender build, with a relatively short trunk, and is adapted for life in tall, dense grass. Its galloping type of locomotion results from the hind quarters being taller than the shoulders. The hoofs are narrow and short, with well-developed lateral digits, rendering these animals well-suited to travelling on soft ground (Flerov, 1952).

The skull of deer is elongated, with maximum width less than half its length. Lacrimal bones are shorter than the orbital cavity diameter. The ethmoidal aperture is variable in size. Intermaxillary bones taper anteriorly without forming blade-shaped projections on their exterior border. Anterior ends of nasal bones are forked, and touch admaxillary bones. The tooth-bearing portion of the facial region is relatively short. The dental formula is i 0/3, c 0/1, p 3/3, m 3/3, total 32 (Flerov, 1952; Korotkevich and Danilkin, 1992).

Antler processes of the frontal bone are slanted backward and upward, with height not exceeding width; they are comparatively far apart, but the distance between inner sides of pedicles is less than 1.5 times their width. Antlers of adults grow faster, attain larger size and are cleaned of velvet two or three weeks earlier than those of subadults. These differences allow adult bucks to occupy territories first (Danilkin, 1992c; Sokolov and Danilkin, 1981).

Capreolus pygargus molts twice a year, in spring and in autumn. Skin thickness on the head and neck varies seasonally in males, but remains the same throughout the year in females. In autumn and in late winter, the skin of both sexes has a maximum thickness of 2.5 mm. In summer, head and neck skin of adult males is 2–5 times thicker (up to 10.5 mm behind the antlers) than on the back and sides. Skin thickening in males coincides with intensification of aggressive behavior during the breeding season and undoubtedly functions to reduce damage to the head region during territorial encounters. A consequence of the skin thickening and enlargement of muscles is that the neck circumference of males in summer is several centimeters greater than the females. The seasonally enlarged sebaceous and sudoriferous skin glands located in the thickened skin of the head and neck, together with interdigital and metatarsal skin glands, produce a secretion used for olfactory marking of territories (Danilkin, 1992c; Sokolov and Danilkin, 1981).

ONTOGENY AND REPRODUCTION. Rut takes place in August and September. Gonad activation in male deer occurs in February. Testis mass is highest in July (30–54 g) and lowest in winter (3–9 g; Pole, 1973; Smirnov, 1978; Sokolov and Danilkin, 1981). Spermatogenesis reaches a peak in July and August. During August, sperm production begins to decline and spermiogenesis is prevalent. Spermatogenesis stops by the end of September and, by late December, there are no live spermatozoa in sexual organs. Mitosis of spermatogonia begins again in April and, by May, there are sufficient numbers of spermatozoa for fertilization of does to occur (Tsaplyuk, 1977).

Female deer are seasonally polyestrous and have a single long mating period. In January, the ovaries contain only atretic follicles. Primary and secondary follicles begin to develop in February and

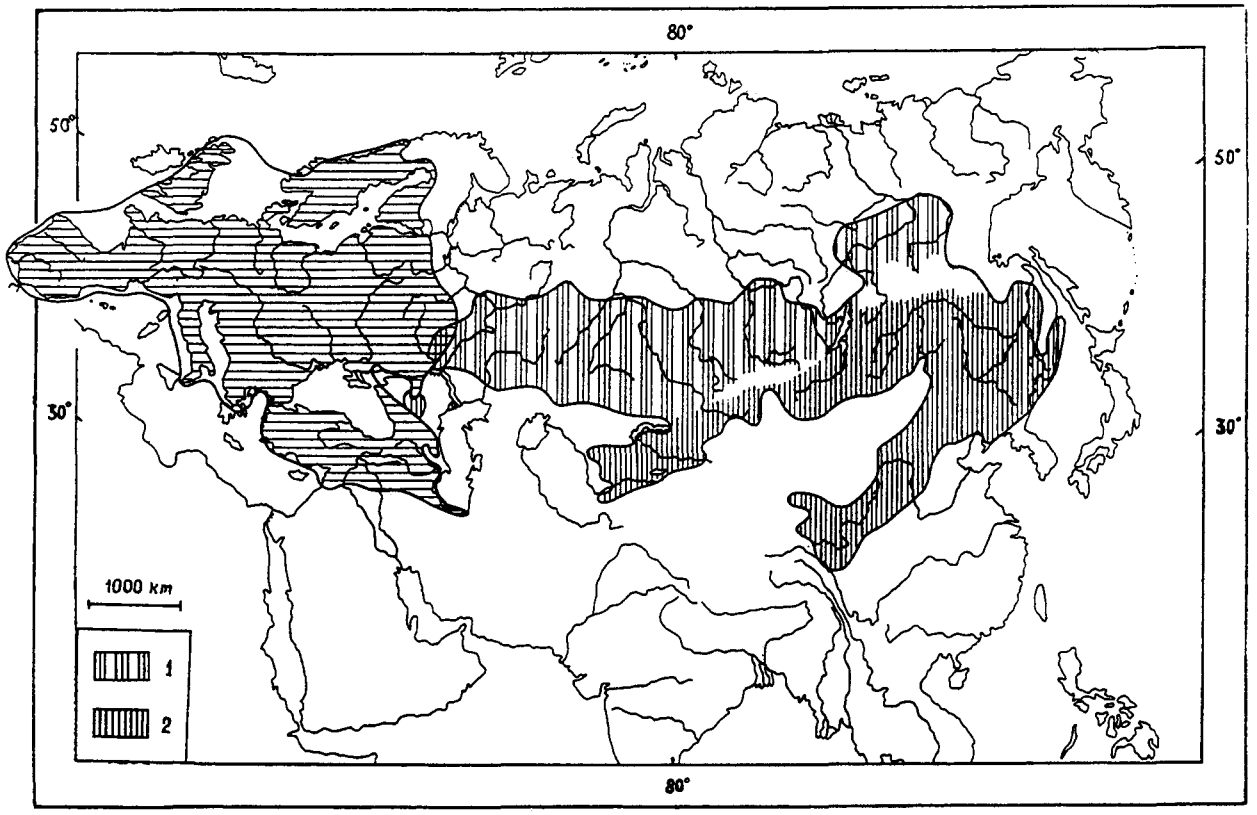

FIG. 3. Modern distribution of *Capreolus* (horizontally hatched area is *C. capreolus*). 1—*Capreolus pygargus pygargus*, 2—*Capreolus pygargus tianschanicus*.

maturation of ovulatory follicles occurs in August. In September and October, the ovaries contain developing yellow bodies, which seem to promote development of the next generation of vesicular follicles and thus support polyestrality. Fertilization of female *C. pygargus* is theoretically possible from May to December, but is much reduced in May–June because most are either in the latter stage of pregnancy or are lactating. Toward the end of the mating period (from October to December), fertilization is difficult owing to cessation of spermatogenesis in males (Tsaplyuk, 1977).

Siberian and European roe deer are the only ungulates that exhibit embryonic diapause, which is probably caused by a shortage of substances triggering and sustaining embryo development. Implantation of the embryo takes place in January (Aitken, 1974, 1981; Tsaplyuk, 1977). Gestation normally lasts 280–300 days (Gromov, 1986; Stubbe and Danilkin, 1992a).

Fawning in *Capreolus pygargus* begins in the second half of May and continues to mid-July (Stubbe and Danilkin, 1992*a*). About a month before fawning, an adult doe separates from its group and occupies a small fawning range that is the same each year and is protected from other females (Sokolov and Danilkin, 1981). Most fawning occurs in daylight. The female gives birth either in a lying or standing position; when several young are born, these two postures may alternate. The first fawn is delivered between 8 and 40 min after the limbs emerge. The second and third young appear at 10 to 40 min intervals. The afterbirth separates 12 to 50 min after the last is born. Normal delivery usually takes a total of 1.5 to 2 h, but can extend over 4 to 5 h (Gromov and Danilkin, 1984; Sokolov and Danilkin, 1981).

Siberian roe deer normally give birth to two young, although rarely one or three may occur (Stubbe and Danilkin, 1992a). Newborn weigh 1.5–2.5 kg, have spotted fur, and eyes are open. As soon as the young is born, it utters gentle squeaks, to which the mother responds with a hissing sound. The mother then lies beside it, removes the remains of the amnionic sac, and spends 5 to 20 min licking it. Caul and grass in the place where her young were lying are immediately eaten by the mother, as is the afterbirth. The young, still wet, noses the mother's body until it finds the udder and then sucks for 2–3 min. The fawn then may move 1–30 m from its mother on its own and lie down in high grass. Some follow their mother who evidently tries to take them from the birth place to different sites (Gromov and Danilkin, 1984; Sokolov and Danilkin, 1981; Sokolov et al., 1985). Although fawns are not weaned until approximately 4–5 months of age, they begin to eat vegetative food in 5–10 days (Sokolov et al., 1985).

During the first days of life, young are helpless and hide when alarmed; they do not attempt to run when approached and even touched, but will squeak when handled. From 3–7 days of age, fawns vocalize and flee if approached to within 1–2 m. At 1–3 weeks of age, the fawn responds this way at a distance of 10 m; thereafter, the young will flee silently if approached at 15–30 m, but will still squeak when caught. In the first 1–2 weeks of age, the female responds to this alarm signal, and to the approach of humans or other animals, with aggressive behavior. The freezing period lasts for about 2.5 to 3 months (Sokolov and Danilkin, 1981).

The development of *C. pygargus* is similar to that of *C. capreolus* (Sokolov and Danilkin, 1981), but when maintained under similar conditions, growth rate of the Siberian roe deer is considerably faster. In captivity, body mass of newborn fawns of Siberian and European roe deer averaged 1,850 g and 1,650 g, respectively. During the growth period, weight gain of Siberian roe deer averaged 6 kg, while that of European roe deer averaged 4 kg per month. By adulthood, *C. capreolus* is approximately 80% as heavy as *C. pygargus* (33 kg and 42 kg, respectively; Gromov, 1988).

Some female deer reach puberty in their first year of life, but the majority do not breed until the second year. Male *C. pygargus* reach puberty in the beginning of their second year of life, although young males rarely have a territory of their own by the rutting period. Consequently the majority of males begin breeding in the third year of life (Pole, 1973; Stubbe and Danilkin, 1992*a*; Tsaplyuk, 1977).

ECOLOGY. Siberian roe deer live in forest and steppe habitats; in forests, they prefer revegetating burns and clearings. They develop high densities (up to 4–12 individuals per 100 ha) in tall-grass meadows and floodplains. In eastern Mongolia, there are steppe populations that dwell in forestless landscape throughout the year, provided there are hills, ravines and tall grass to provide cover (Zejda and Danilkin, 1992). *C. pygargus* is adapted to severe weather

extremes and inhabits areas where the temperatures range from <−60°C (winter in Yakutia) to >40°C (summer in central Asia; Danilkin, 1992*d*).

Deer consume over 600 species of plants, the most important being herbaceous dicotyledons (58%), monocotyledons (16%) and woody species (22%; Holisova et al., 1992). Average mass of stomach contents was 2.5 kg (1–4.7 kg), ranging from 2.2 kg (1–3.9 kg) when vegetation was actively growing to 3.2 kg (2.1–4.7 kg) when the ground was snow-covered (Sokolov and Danilkin, 1981). Percentages of some plant species in the diet of *C. pygargus* vary greatly from season to season (Darman, 1986; Smirnov, 1978). A drastic winter reduction in assortment and quantity of food coincides with lowering of metabolic rate (Kholodova, 1986). In summer, deer visit natural salt deposits (Fetisov, 1953). Water is obtained from moisture-rich foods, allowing deer to live dozens of kilometers from natural sources, as is the situation in the Mongolian steppes (Danilkin and Dulamtseren, 1981).

The sex ratio and age structure of populations of Siberian and European roe deer do not differ significantly. The life-span under natural conditions normally does not exceed 10 years. The sex ratio of young and adult of Siberian roe deer ranges from 1:1 to 1:1.3 in favor of females (Averin, 1949; Bromlei and Kucherenko, 1983; Danilkin, 1992b; Darman, 1986; Lavov, 1971; Pole, 1973; Smirnov, 1978). Immediately after the fawning period, young may constitute up to 50% of the population. By autumn, various populations were composed of 20%–48% fawns, 15–23% subadultus, and >34% adults (Danilkin, 1992b; Darman, 1986; Dvornikov, 1984; Kiselev, 1979; Lavov, 1966, 1971; Smirnov, 1978; Sokolov and Danilkin, 1981). The sex and age structure of exploited populations may vary greatly depending on relative hunting pressures on sex-age groups.

The spatial structure of populations of Siberian roe deer undergoes considerable change throughout the year, but is relatively stable within two long periods: summer (reproductive and territorial period), when animals are solitary and evenly dispersed; and winter (non-territorial period), when animals aggregate in feeding ranges. In spring adult males occupy and defend territories (10–170 ha) that are the same each year. Sizes of the females seasonal home ranges varies from 2–7 ha in the fawning period to 180 ha towards the end of the summer season (Smirnov, 1978; Sokolov and Danilkin, 1981). In the reproductive period, the core of spatial structure of the population is formed by home ranges of the "composite family" consisting of several closely related does and their offspring existing in the territory of a male. In winter, intrapopulation spatial structure varies from region to region. There are populations that migrate seasonally and withdraw fully from their summer range, populations that remain in one place throughout the year, and populations that include both settled animals and seasonal migrants whose numbers depend on snow depth. Winter home ranges of individuals and groups overlap widely (Danilkin, 1992b).

In many regions of Asia, seasonal mass migrations away from areas with deep snow are ultimately a response to lack of food (Averin, 1949; Fetisov, 1953; Nasimovich, 1955; Sabaneev, 1875; Sobanski, 1987; Subbotin, 1973; Ushkov, 1954). However, most animals migrate in September, when there is no snow, daytime temperatures are above freezing, and forage is abundant. The first frost is the most probable signal for autumnal migration. Having reached winter quarters, migrants usually remain until spring. The mass return migration of deer in spring takes place at the end of March and beginning of April, but some individuals start their movement back to summer ranges as early as December and January. Migration is complete in April and May (Danilkin, 1992a; Danilkin et al., 1992a). Siberian roe deer normally migrate in family groups. During the peak of migration they form herds of several dozens to hundreds of individuals (Barancheyev, 1962). Migrations are not observed in regions with little snow.

Migration routes may be as long as 500 km (Bromlei and Kucherenko, 1983; Kucherenko, 1976; Rakov, 1965). Routes followed by individuals are the same for many years. The mean speed of animals during their autumnal migration is 6.1 km per day (maximum is 26 km per day); in spring, speed averages 3.8 km per day. *C. pygargus* travel at any time of day, but more frequently in morning. The daily sex-age ratio of migrant animals is approximately the same as the sex-age structure of the population. As a rule, migrant group leaders are adult females. Most adult males migrate alone or in groups consisting only of males (Danilkin et al., 1992a).

The Siberian roe deer is mainly preyed upon by *Canis lupus* and *Felis lynx*. Predation by wolves increases dramatically when snow is deep and has a frozen crust, conditions which make prey movement difficult. In the Far East, approximately 3,500 Siberian roe deer are killed every year. In forest biocenoses, 20–25% of the population is destroyed (Bromlei and Kucherenko, 1983; Kucherenko, 1976, 1979; Kucherenko and Shvets, 1977; Kucherenko and Zubkov, 1980). In the northern Trans-Baikal Area, wolves kill 28.5 to 32.4% of the autumn stock, taking animals of any sex and age (Lavov, 1982). In eastern Siberia, they follow herds of *C. pygargus* during migration (Fetisov, 1953). In the Ural Mountains, remains of deer were found in 95.9% of predator's excreta (Averin, 1949; Filonov, 1974). In some regions, predation by the lynx exceeds that of the wolf; in the Amursk Region alone, 6,000–10,000 Siberian roe deer are killed by lynx yearly (Bromlei and Kucherenko, 1983; Dimin, 1975; Dimin and Yudakov, 1967; Kucherenko and Shvets, 1977).

Climatic factors not only determine the distribution of Siberian roe deer, but also affect numbers. Severe winters take especially heavy tolls because of combined effects of weather, increased predation, and hunting. An extremely snowy winter in 1972/1973 in the Far East provides an illustration of the impact of severe weather. Snow fell early in autumn and reached a depth of 1–1.5 m. Animals were unable to reach their wintering ranges and many were drowned crossing rivers in which thin ice was hidden by a thick layer of snow. Distressed survivors were killed by poachers and predators, died of famine, or froze to death in herds of 20–30 animals. By spring, only 25–33% of the population survived (Kucherenko and Shvets, 1977; Shvets, 1975). Similar episodes have occurred in 1940/1941 in the Ural Mountains (Filonov, 1974; Ushkov, 1954), and in Kazakhstan in winters of 1945/1946, 1959/1960, 1965/1966, and 1975/1976 (Sludski et al., 1984).

Mortality from disease is relatively rare since population densities are usually low. The main infectious diseases are pasteurellosis, foot-and-mouth disease and anthrax. The most important parasites are as follows: *Fasciola hepatica, Dicrocoelium lanceatum, Liorchis scotiae, Avitellina pygargi, Taenia cervi, Taenia hydatigena, Nematodirus fillicollis, Nematodirus oiratianus, Spiculopteragia alcis, Trichocephalus capreoli, Skrjabinema ovis, Parabronema skrjabini, Protostrongylus Kochi, Bunostomum trigonocephalum, Setaria altaica, Setaria tundra, Setaria capreola, Capreocaulus capreoli,* and *Dermacentor daghestanicus, Dermacentor marginatus, Dermacentor silvarum, Haemaphysalis concinna, Rhipicephalus pumilio, Ixodes persulcatus, Lipoptena cervi, Lipoptena fortisetosa, Pharingomyia picta, Cephenomyia stimulator, Hypoderma capreola* (Sludski et al., 1984; Smirnov, 1978).

The most important cause of mortality of deer is hunting. Legal shooting itself has little impact, but in combination with poaching, losses from hunting may exceed those from all other causes (Danilkin and Blusma, 1992).

Major competitors of *C. pygargus* are domestic ungulates (Lavov, 1978; Nikolayev, 1982), moose (*Alces alces*) and red deer (*Cervus elaphus*; Danilkin and Dulamtseren, 1981; Kiselev, 1976). Decline of Siberian roe deer populations is correlated with increases in red deer density, as exemplified by the change in numbers of Siberian roe deer and Altai red deer (*Cervus elaphus sibiricus*) in the Bogdo-Ula Preserve, Mongolia (Kozlov, 1924). Between the 1920s and 1950s Siberian roe deer were numerous, whereas Altai red deer were sparse. By mid-1980s, the red deer population density had increased to 55–90 animals per 1,000 ha, and Siberian roe deer had disappeared in the preserve (Danilkin and Dulamtseren, 1981).

Some ungulates may have a positive effect on densities of *C. pygargus*. Digging snow (in the Asian portion of the area) in winter, boar (*Sus scrofa*) and domestic ungulates prepare feeding places for roe deer. In numerous parts of Russia where snow is deep, survival of deer in winter strongly depends on other species (deer, elk, and boar) to make paths in snow, facilitating movement from one biotope to another (Danilkin and Blusma, 1992).

The total number of Siberian roe deer is about 1 million in a range of 7.4 million square km. In most regions the population density is one or two orders of magnitude lower than that of the European roe deer, mostly due to poaching, predation, and high mortality during winters with heavy snow (Danilkin, 1989*a*; Danilkin and Blusma, 1992; Stubbe and Danilkin, 1992*b*). The highest recorded population density was in the last century when up to 500,000 were taken annually in Russia alone (Turkin and Satunin, 1902).

BEHAVIOR. Siberian roe deer fawns display reactions to various environmental stimuli (visual inspection, sniffing, listening)

from birth. At two weeks of age, juveniles' orientative-exploratory reactions do not differ from those of adults. Newborns exhibit few comfort behaviors. The first attempts at body licking are recorded at 4–6 days of age, and at 3–4 weeks of age, young care for their own coats. However until 2–2.5 months of age, this function is performed mostly by the mother during feeding periods. Her lickings are especially long and thorough in their first fortnight when fawns have difficulty excreting on their own. Play behavior is observed in fawns from 3 days of age. Sexual play behavior in young males is recorded from 1.5–2 months of age. In this period, they also develop activities resembling marking. At 4 months of age, their play exhibits the whole range of postures peculiar to the antagonistic behavior of adult males. By 2.5–3 months of age, offspring have learned all main forms of behavior from their parents; however, juvenile territorial and sexual behavior greatly differs from adult behavior (Sokolov et al., 1985).

In their first days, fawn active periods coincide with feeding bouts, each lasting for about 30 min. Young stand only when their mother comes to them and lie down as soon as she goes away, but as early as their second week, they walk several minutes before and after suckling without their mother beside them. In the first two or three weeks, the female feeds her offspring one at a time, alternating between them and only rarely feeding the same fawn during two sequential bouts. Later, the mother mostly feeds her young together, but the feeding periodicity remains. The number of meals of milk varies with fawn number: in the first month, it may be as high as 5 to 9 meals per day; in the second month, it is 2–4 meals per day; and later it decreases to 1 or 2 meals, but the time of family members' joint activities increases. From 1 month of age, length of active periods is 1–1.5 h, and from two months, length is 1.5–2 h long; 30-40% of active periods is spent grazing around their beds in the mother's absence. Although the number of milk meals gradually decreases, the number of active periods (5–7 per day) remains nearly the same. Synchronization of family member activities takes place only when young are more than 2.5–3 months of age (Danilkin, 1992*c*; Sokolov et al., 1985).

Activity of Siberian roe deer may vary within the year, season, and time of day, depending on sex, age, degree of anxiety, climate, and other environmental factors. The daily rhythm includes alternating moving about and grazing with rest and mastication, usually from 4 to 7 times a day. The morning and evening activity periods are longest and occur with most predictable timing. Individuals and groups are most active at sunrise and sunset. Activity rhythms of group members are synchronous, apparently the result of individuals following the behavior of a leader individual (Smirnov, 1978; Sokolov and Danilkin, 1981).

Siberian roe deer are aggressive mainly during the reproductive period. Social relationships between females and their adult progeny are ended 2–4 weeks before a new generation is born. The separation is caused by increased aggressiveness of mothers toward other animals in their fawning ranges. Aggressive behavior is expressed most strongly toward individuals approaching 1–2-week-old fawns. In general, male *C. pygargus* are more aggressive than females. The onset of aggressive behavior coincides with removal of velvet from antlers and marking activities. Most aggressive encounters take place during seizure of territories and before rut. Adult males are especially intolerant of animals without territories. The emigration of young animals from their birthplace is largely caused by aggressiveness of adult males who drive them from their territories. Conflicts between neighboring territorial males are comparatively rare (Smirnov, 1978; Sokolov and Danilkin, 1981). After the reproductive period aggressiveness of roe deer declines to the extent that, in winter, all group members may feed together without being noticeably antagonistic.

From spring through autumn, males provide their ranges with olfactory and visual marks. The olfactory marks are made with a secretion of head skin glands, which greatly swell in summer. The secretion is applied by rubbing the forehead, cheeks and neck against trees, shrubs and high grasses. Visual marks are trees frayed with antlers. Other substances that may be used in signalling are urine, feces, and saliva, as well as scented secretions of sexual organs, metatarsal and interdigital glands, and glandular complexes in the skin on distal sections of the metatarsals and metacarpals (Sokolov and Danilkin, 1981).

In the rutting period, the territorial system is not generally violated. The rut of deer usually lasts for 2 to 5 days. The male nearly stops feeding, becomes careless and does not leave the doe even in apparent danger. In the first day of the rutting period, males, especially young ones, are quite aggressive toward females and may strike them with antlers. After a lengthy chase in large circles, the tired female begins running around trees, shrubs, high hummocks, and pits; when exhausted, the female stops and allows the equally tired male to mate with her. Subsequently, both lie down to rest. Running through the same place repeatedly results in characteristic paths with a circular or figure-eight configuration (Sokolov and Danilkin, 1981).

Vocal signals play an important role in the social life of roe deer. Six main types of signals can be discerned: squeaking (or whistling), rasping (panting), barking, whining, screaming, and sounds of non-vocal origin. At an early age, *C. pygargus* seemingly has only one type of acoustic signal—squeaking (soft and loud). All signals except whining are the same in males and females. Vocalizations are similar to those of European roe deer and have the same functional significance, a reflection of phylogenetic relatedness. However, *C. capreolus* males are not known to produce a whining sound (Sokolov and Danilkin, 1981) and paired squeaks have not been recorded in females of European roe deer. In general, sounds of European roe deer are more high-pitched and young produce squeaks with different characteristics (Sokolov et al., 1987).

In Siberian roe deer, orientative-exploratory and defensive behaviors are a series of separate elements: orientation posture, signal hops, fear reaction, moving close to other individuals, warning of danger by running, searching for and precisely identifying the threat, fleeing, and freezing. In various situations, only some of these elements are displayed, and may be given in a different order. Twenty-five to 50% of active periods are spent in orientative-exploratory behavior. Although hearing and vision are used to generally identify threats, olfaction is the primary sensory modality for gaining precise information. In certain situations, individuals will move downwind in order to locate and indentify an odor. When danger is apparent, young lie down and press their heads to the ground; adults either stand still with their heads lowered or, in the case of dwellers of open steppe biotopes, lie down like fawns. In a group of Siberian roe deer the flight of one member causes a similar reaction by others (Smirnov, 1978; Sokolov and Danilkin, 1981).

GENETICS. *Capreolus pygargus* has a diploid number of 71–84 chromosomes; this number includes 1–14 B-chromosomes in addition to 70 chromosomes of the main set. All autosomes are acrocentric, whereas the X-chromosome is submetacentric (Danilkin, 1985b, Sokolov et al., 1978). Karyotypes are both stable and mosaic (with a different number of B-chromosomes in the same individual and in different individuals in the same population; Danilkin and Baskevich, 1987). Hybrids derived from crossing *C. capreolus* and *C. pygargus* inherit B-chromosomes (Zernahle, 1980).

Although interbreeding between European and Siberian roe deer is possible, most hybrid males are sterile and many small European roe deer females either die giving birth to large hybrid fetuses or give birth to dead young. Only about 20% of females in these experiments could normally (without human assistance) produce live hybrid fawns (Danilkin, 1986; Sokolov and Gromov, 1985; Stubbe and Bruchholz, 1980).

REMARKS. The Siberian roe deer was called *pygargus* for the following reason. When travelling in the Russian Empire, in October 1768, P. S. Pallas sighted in the Trans-Volga Area strange animals whose "hind quarters were covered by a large white patch extending up to the very back, by which these wild goats could be regarded as Pygargus of the ancients" (Pallas, 1809).

Authorities disagree about the intraspecific taxonomy of *Capreolus pygargus*. Different authors distinguish 2 to 5 subspecies and indicate different borders of their ranges (Barishnikov et al., 1981; Ellerman and Morrison-Scott, 1951; Flerov, 1952; Heptner et al., 1961; Sokolov and Gromov, 1988, 1990; Stubbe, 1990), but most do not provide diagnoses of forms accorded subspecific status. The systematic status of *C. p. caucasicus* is unclear (Flerov, 1952; Heptner et al., 1961). At the present time, *C. p. caucasicus* is not found on the northern slopes of the Caucasus, which is now included in the range of *C. capreolus* (Danilkin and Markov, 1985).

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